MINIMIZING INBREEDING IN TETRAPLOIDS DERIVED THROUGH SEXUAL POLYPLOIDIZATION

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Abstract

Diploid ($2n = 2x = 24$) potato (*Solanum*) species that produce 2n gametes are being utilized in potato breeding programs. Three breeding schemes involving these diploids are presently used by potato breeders to transfer this genetic material from diploid parents to their tetraploid offspring. Derived tetraploids may arise through tetraploid x diploid, tetraploid x haploid-species, or diploid x diploid hybridizations. The inbreeding coefficient of derived tetraploids is a complex function of the coancestry of the parents, the inbreeding of the parents, the coefficient of double reduction in the tetraploid parent, and the frequency of single exchange tetrads in the diploid parent(s), and it depends on the mechanism of 2n gamete formation. For the two breeding strategies involving tetraploid female parents, there is less inbreeding in the derived tetraploid from a diploid parent producing 2n pollen by first division restitution than 2n pollen by second division restitution when the frequency of single exchange tetrads in the diploid is less than ⅔. In bilateral sexual polyploidization, the inbreeding coefficient of a derived tetraploid for a given set of parents from a first division x first division restitution cross is less than the inbreeding coefficient of a second division x first division restitution cross which is less than the inbreeding coefficient of a second division x second division cross when the frequency of single exchange tetrads is less than ⅔.

Compendio

Especies diploides ($2n = 2x = 24$) de papa (*Solanum*) que producen gametos 2n están siendo utilizadas en programas de mejoramiento del cultivo. Tres esquemas de mejoramiento que incluyen a estos diploides están en la actualidad siendo usados por los mejoradores de papa para transferir este material genético de padres diploides a su descendencia tetraploide. Los tetraploides obtenidos pueden surgir de hibridaciones de tetraploides x diploides, tetraploides x especies haploides o de diploides x diploides. El

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coeficiente de retrocruzamiento de los tetraploides obtenidos es una función compleja de la coascendencia de los padres, el retrocruzamiento de los padres, el coeficiente de doble reducción en los padres tetraploides y la frecuencia del intercambio de tetradas individuales en el o los padres diploides y ello depende en el mecanismo de la formación de los gametos 2n. Para las dos estrategias de mejoramiento incluyendo madres tetraploides, existe menos retrocruzamiento en los tetraploides obtenidos de un padre diploide produciendo polen 2n por restitución de la primera división que polen 2n por restitución en la segunda división cuando la frecuencia de tetradas de intercanbio individual en los diploides es menor de ⅔. En poliploidización sexual bilateral, el coeficiente de retrocruzamiento de un tetraploide obtenido para un grupo dado de padres derivados de un cruzamiento de primera división x restitución de primera división es menor que el coeficiente de retrocruzamiento de un cruzamiento de segunda división x restitución de primera división que a su vez es menor que el coeficiente de retrocruzamiento de un cruzamiento de segunda división x segunda división cuando la frecuencia de tetradas de intercambio individual es menor de ⅔.

Introduction

Inbreeding depression in potatoes at the diploid (1) and tetraploid (10, 11) level have been reported and discussed (8). Thus, breeding strategies should be aimed at reducing the amount of inbreeding present in potato populations.

Through the production of 2n gametes (2, 9), diploid (2n = 2x = 24) potato species are being widely utilized in potato breeding programs to introduce new genes into the genetic base of tetraploid (2n = 4x = 48) potatoes. Derived tetraploids may arise by hybridizations between: 1) tetraploids and 2n pollen producing diploids (6); 2) tetraploids and 2n pollen producing haploid-species hybrids (5); or 3) 2n ovule and 2n pollen producing diploids (7).

Haynes (4) has recently derived the inbreeding coefficient for derived tetraploids produced by these three methods. These inbreeding coefficients were shown to be functions of the coefficient of double reduction (α) in the tetraploid parent where applicable, the frequency of single exchange tetrads (β) in the diploid or haploid-species hybrid, the coefficient of coancestry (θ) between the parents, and the inbreeding coefficients (F) of the parents, and they depend on the mechanism of 2n gamete formation.

The purpose of this article is to define conditions for a given set of parents: 1) where either first division restitution or second division restitution in the diploid will lead to less inbreeding in a derived tetraploid from tetraploid x diploid or tetraploid x haploid-species hybridization, and 2) that lead to less inbreeding in derived tetraploids from bilateral sexual polyploidizations, *i.e.*, diploid x diploid hybridizations.

Methods and Results

Tetraploid x Diploid Hybridizations—Haynes (4) has previously calculated the inbreeding coefficient for two types of tetraploid x diploid hybridizations that produce derived tetraploids. The inbreeding coefficient for a derived tetraploid produced by a tetraploid x FDR 2n pollen producing diploid (FDR2x) hybridization is:

$$F_{4x\ X\ FDR2x} = (1/6)[\alpha + (1 - \alpha)F_T + 4\theta_{TZ} + \beta/2 + (1 - \beta/2)F_Z]$$

The inbreeding coefficient for a derived tetraploid produced by a tetraploid x SDR 2n pollen producing diploid (SDR2x) hybridization is:

$$F_{4x\ X\ SDR2x} = (1/6)[\alpha + (1 - \alpha)F_T + 4\theta_{TZ} + 1 - \beta + \beta F_Z]$$

where

β = frequency of single exchange tetrads in the diploid parent
α = coefficient of double reduction in the tetraploid parent
F_T = inbreeding coefficient of the tetraploid parent
F_Z = inbreeding coefficient of the diploid parent
θ_{TZ} = coefficient of coancestry between the tetraploid and diploid parent

We may ask under what conditions would a 4x X FDR2x mating show less inbreeding than a 4x X SDR2x mating? To answer this question, we simplify the following inequality:

$$F_{4x\ X\ FDR2x} < F_{4x\ X\ SDR2x}$$

Thus,

$$(1/6)[\alpha + (1 - \alpha)F_T + 4\theta_{TZ} + \beta/2 + (1 - \beta/2)F_Z] <$$
$$(1/6)[\alpha + (1 - \alpha)F_T + 4\theta_{TZ} + 1 - \beta + \beta F_Z]$$

which simplifies to:

$$F_Z(2 - 3\beta) < 2 - 3\beta$$

Now, this inequality depends on the quantity $2 - 3\beta$.
However, by definition,

$$0 \leq F_Z \leq 1$$

which implies that

$$2 - 3\beta > 0$$

Otherwise, the inequality could not hold.

Thus, $\beta < 2/3$.

Therefore, when $\beta < 2/3$, the inbreeding coefficient of the derived tetraploid from a 4x X FDR2x mating will always be less than the inbreeding coefficient of the derived tetraploid from a 4x X SDR2x mating. Conversely, when $\beta > ⅔$, the inbreeding coefficient of the derived tetraploid from a 4x X SDR2x mating will always be less than the inbreeding coefficient of the derived tetraploid from a 4x X FDR2x mating. Lastly, when $\beta = ⅔$, the inbreeding coefficient of the derived tetraploid is the same for either a 4x X FDR2x or 4x X SDR2x mating.

Tetraploid x Haploid-species Hybridizations — Haynes (4) has previously calculated the inbreeding coefficient for two types of tetraploid x haploid-species hybridizations that produce derived tetraploids. The inbreeding coefficient for a derived tetraploid produced by a tetraploid X FDR 2n pollen producing haploid-species hybridization (FDR H-S) is:

$$F_{4x\ X\ FDR\ H\text{-}S} = (1/6)\,[\alpha + (1 - \alpha)F_{T2} + 2\theta_{T1T2} + \beta/2]$$

The inbreeding coefficient for a derived tetraploid produced by a tetraploid x SDR 2n pollen producing haploid-species hybridization (SDR H-S) is:

$$F_{4xX\ FDR\ H\text{-}S} = (1/6)\,[\alpha + (1 - \alpha)F_{T2} + 2\theta_{T1T2} + 1 - \beta]$$

where

α = coefficient of double reduction in the tetraploid parent
β = frequency of single exchange tetrads in the haploid-species hybrid
F_{T2} = inbreeding coefficient of the tetraploid parent
θ_{T1T2} = coefficient of coancestry between the tetraploid and haploid-species parent

We may ask under what conditions would a 4x X FDR H-S mating show less inbreeding than a 4x X SDR H-S mating? To answer this question, we simplify the following inequality:

$$F_{4x\ X\ FDR\ H\text{-}S} < F_{4x\ X\ SDR\ H\text{-}S}$$

Thus,

$$(1/6)[\alpha + (1 - \alpha)F_{T2} + 2\theta_{T1T2} + \beta/2] <$$
$$(1/6)[\alpha + (1 - \alpha)F_{T2} + 2\,\theta_{T1T2} + 1 - \beta]$$

which simplifies to:

$$\beta < ⅔$$

Therefore, when $\beta < ⅔$, the inbreeding coefficient of the derived tetraploid from a 4x X FDR H-S mating will always be less than the inbreeding coefficient of the derived tetraploid from a 4x X SDR H-S mating. Conversely, when $\beta > ⅔$, the inbreeding coefficient of the derived tetraploid from a 4x X SDR H-S mating will always be less than the inbreeding coefficient of the derived tetraploid from a 4x X FDR H-S mating. Lastly when $\beta = ⅔$, the inbreeding coefficient of the derived tetraploid is the same for either a 4x X FDR H-S or 4x X SDR H-S mating.

Diploid x Diploid Hybridizations—Haynes (4) has also calculated the inbreeding coefficient for three types of diploid x diploid hybridizations that produce derived tetraploids: (1) FDR x FDR 2n gamete producing hybridizations; (2) SDR x SDR 2n gamete producing hybridizations; and (3) SDR x FDR 2n gamete producing hybridizations. The inbreeding coefficient for the first case is:

$$F_{FDR2x \text{ X } FDR2x} = (1/6)[(\tfrac{1}{2})(\beta_{Z1} + \beta_{Z2}) + (1 - \beta_{Z1}/2)F_{Z1} + (1 - \beta_{Z2}/2)F_{Z2} + 4\theta_{Z1Z2}]$$

The inbreeding coefficient for the second case is:

$$F_{SDR2x \text{ X } SDR2x} = (1/6)[2 + \beta_{Z1}(F_{Z1} - 1) + \beta_{Z2}(F_{Z2} - 1) + 4\theta_{Z1Z2}]$$

And, the inbreeding coefficient for the third case is:

$$F_{SDR2x \text{ X } FDR2x} = (1/6)[1 - \beta_{Z1} + \beta_{Z1}F_{Z1} + \beta_{Z2}/2 + (1 - \beta_{Z2}/2)F_{Z2} + 4\theta_{Z1Z2}]$$

where

β_{Z1} = frequency of single exchange tetrads in the female parent
β_{Z2} = frequency of single exchange tetrads in the male parent
F_{Z1} = inbreeding coefficient of the female parent
F_{Z2} = inbreeding coefficient of the male parent
θ_{Z1Z2} = coefficient of coancestry between the female and male parent.

By assuming that the frequency of single exchange tetrads is the same in the female and male parents, we may ask under what conditions would a SDR2x X FDR2x mating show less inbreeding than a FDR2x X FDR2x mating? To answer this question, we simplify the following inequality:

$$F_{SDR2x \text{ X } FDR2x} < F_{FDR2x \text{ X } FDR2x}$$

Thus,

$$(1/6)[1 - \beta + \beta F_{Z1} + \beta/2 + (1 - \beta/2)F_{Z2} + 4\theta_{Z1Z2}] <$$
$$(1/6)[(\tfrac{1}{2})(2\beta) + (1 - \beta/2)F_{Z1} + (1 - \beta/2)F_{Z2} + 4\theta_{Z1Z2}]$$

which simplifies to:

$$F_{Z1}(3\beta - 2) < 3\beta - 2$$

Now, this inequality depends on the quantity $3\beta - 2$.

However, by definition

$$0 \leq F_{Z1} \leq 1$$

which implies that

$$3\beta - 2 > 0$$

Otherwise, the inequality could not hold.

Thus, $\beta > 2/3$.

Therefore, when $\beta < 2/3$, the inbreeding coefficient of the derived tetraploid from a FDR2x X FDR2x mating will always be less than the inbreeding coefficient of the derived tetraploid from a SDR2x X FDR2x mating. Conversely, when $\beta > 2/3$, the inbreeding coefficient of the derived tetraploid from a SDR2x X FDR2x mating will always be less than the inbreeding coefficient of the derived tetraploid from a FDR2x X FDR2x mating. Lastly, when $\beta = 2/3$, the inbreeding coefficient of the derived tetraploid is the same for either a SDR2x X FDR2x or FDR2x X FDR2x mating.

Next, we may ask under what conditions would a SDR2x X SDR2x mating show less inbreeding than a SDR2x X FDR2x mating? To answer this question, still assuming that the frequency of single exchange tetrads is the same in the female and male parents, we simplify the following inequality:

$$F_{SDR2x\ X\ SDR2x} < F_{SDR2x\ X\ FDR2x}$$

Thus,

$$(1/6)[2 + \beta(F_{Z1} - 1) + \beta(F_{Z2} - 1) + 4\theta_{Z1Z2}] <$$
$$(1/6)[1 - \beta + \beta F_{Z1} + \beta/2 + (1 - \beta/2)F_{Z2} + 4\theta_{Z1Z2}]$$

which simplifies to:

$$F_{Z2}(3\beta - 2) < 3\beta - 2$$

Now, this inequality depends on the quantity $3\beta - 2$.

However, by definition

$$0 \leq F_{Z2} \leq 1$$

which implies that

$$3\beta - 2 > 0$$

Otherwise, the inequality could not hold.

Thus, $\beta > 2/3$

Therefore, when $\beta < 2/3$, the inbreeding coefficient of the derived tetraploid from a SDR2x X FDR2x mating will always be less than the inbreeding coefficient of the derived tetraploid from a SDR2x X SDR2x mating. Conversely, when $\beta > 2/3$, the inbreeding coefficient of the derived tetraploid from a SDR2x X SDR2x mating will always be less than the inbreeding coefficient of the derived tetraploid from a SDR2x X FDR2x mating. When $\beta = 2/3$, the inbreeding coefficient of the derived tetraploid is the same for either a SDR2x X SDR2x or SDR2x X FDR2x mating.

Finally, we may ask under what conditions would a SDR2x X SDR2x mating show less inbreeding than a FDR2x X FDR2x mating? The answer is implied by the two previous results. When $\beta < 2/3$, $F_{FDR2x\ X\ FDR2x} < F_{SDR2x\ X\ FDR2x}$ and $F_{SDR2x\ X\ FDR2x} < F_{SDR2x\ X\ SDR2x}$. Therefore, when $\beta < 2/3$, the inbreeding coefficient of the derived tetraploid from a FDR2x X FDR2x mating will always be less than the inbreeding coefficient of the derived tetraploid from a SDR2x X SDR2x mating. Conversely, when $\beta > 2/3$, the inbreeding coefficient of the derived tetraploid from a SDR2x X SDR2x mating will always be less than the inbreeding coefficient of the derived tetraploid from a FDR2x X FDR2x mating. When $\beta = 2/3$, the inbreeding coefficient of the derived tetraploid is the same for either a SDR2x X SDR2x or FDR2x X FDR2x mating.

Discussion

For a given set of parents in which derived tetraploids arise from either tetraploid X diploid or tetraploid X haploid-species hybridizations, inbreeding in the derived tetraploid will be minimized when the frequency of single exchange tetrads in the diploid or haploid-species parent is less than ⅔ for 2n pollen produced by a first division restitution mechanism. When the frequency of single exchange tetrads in the diploid or haploid-species parent is greater than ⅔, inbreeding will be minimized when 2n pollen is produced by a second division restitution mechanism. When the frequency of single exchange tetrads in the diploid or haploid-species parents equals ⅔, the amount of inbreeding will be the same for 2n pollen produced by either a first division or a second division restitution mechanism.

In bilateral sexual polyploidization, under the assumption that the parents were unrelated and not inbred, Haynes (4) has shown that the maximum value of the inbreeding coefficient for a: 1) FDR2x X FDR2x cross is equal to 1/6, 2) SDR2x X FDR2x cross is equal to ¼, and 3) SDR2x X SDR2x cross is equal to ⅓. This work has shown that for a given set of parents, regardless of the level of inbreeding in the parents or their coancestry, the inbreeding coefficient of a FDR2x X FDR2x cross is less than a SDR2x X FDR2x cross when the frequency of single exchange tetrads in the diploid parents is less than ⅔. Similarly, under these same conditions, the inbreeding coefficient of a SDR2x X FDR2x cross is less than a SDR2x X SDR2x cross. When the frequency of single exchange tetrads in the diploid parents equals ⅔, the inbreeding coefficient is the same for FDR2x X FDR2x, SDR2x X FDR2x, and SDR2x X SDR2x crosses. When the frequency of single exchange tetrads in the diploid parents is greater than ⅔, there is less inbreeding in a SDR2x X SDR2x cross, followed by a SDR2x X FDR2x cross, followed by a FDR2x X FDR2x cross.

Regardless of the breeding strategy used to introduce genetic material from the diploid level to the tetraploid level, the point at which the frequency of single exchange tetrads in the diploid parent(s) equals ⅔ is a critical one in determining which mode(s) of 2n gamete formation lead to less inbreeding. Presumably, if the genes for the trait of interest are located on the distal end of the chromosome(s), there could be less inbreeding for this trait under SDR mechanisms since the probability that the frequency of single exchange tetrads exceeds ⅔ with respect to the locus in question would be greater than if the genes were proximally located.

Limited data to date (3) suggest that quantitative trait loci in potatoes are scattered across several chromosomes. Factors that Haynes (4) has previously identified as important in determining the amount of inbreeding for a given locus, namely, the frequency of single exchange tetrads in the diploid parents, the coefficient of double reduction in the tetraploid parents, the coefficient of coancestry of the parents, the level of inbreeding in the parents, and the mechanism of 2n gamete formation will also be important in determining an overall level of inbreeding in the derived tetraploid. This overall level of inbreeding can be extremely complex given that the frequency of single exchange tetrads, the coefficient of double reduction, the coefficient of coancestry, and the level of inbreeding can be different for every individual locus involved in quantitative trait loci. Such complexity is beyond the scope of this work. However, consideration of the level of inbreeding at a single locus has identified many factors that should be considered in the attempt to minimize inbreeding.

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